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Biodiversity: Complementary canopies

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Abstract: Physical complementarity among trees in the use of vertical space increases productivity due to species-specific differences and plasticity in crown architecture.

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1 Biodiversity

2

3 **Complementary canopies**

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12 **Old (with your corrections): Physical complementarity among trees in the use of**
13 **vertical space increases productivity due to species-specific differences and plasticity in**
14 **crown architecture,**

15

16 A large number of biodiversity experiments have shown positive effects of plant species
17 richness on plant biomass production¹. This has been theoretically explained by differences
18 among species in the use of resources such as light and soil nutrients, but empirical evidence
19 for such niche complementarity or division of labor among plant species has rarely been
20 found, and even then solely in grassland ecosystems². Writing in this issue of *Nature Ecology*
21 *& Evolution*, Williams et al.³ demonstrate physical complementarity among trees in the use
22 of vertical space, confirming that crown complementarity is an important mechanism for
23 enhancing primary productivity in forests

24 The hypothesis that complementarity among species causes positive biodiversity
25 effects at the ecosystem level rests on the assumption that no single species is able to acquire
26 all resources in the environment as efficiently as an assemblage of different species can. For
27 example, even though a single species can grow leaves in different canopy layers, it is likely
28 that another species better adapted to low light can fill lower canopy layers. This occupation
29 of different niches becomes possible when the range of available leaf adaptations to different
30 light levels is greater in mixed species stands than in monocultures. Even though it seems
31 obvious that physical complementarity among trees should be greater in mixed-species
32 communities, there have been very few experimental tests of this effect⁵ and no tests of
33 whether such physical complementarity indeed promotes ecosystem functioning. One reason
34 for this lack of evidence is that biodiversity experiments typically compare a limited number
35 of different species combinations with a given species richness, making it difficult to separate
36 the effects of physical complementarity from the effect of species richness. In contrast, the

37 study of Williams et al. focused on a larger number of species combinations at two levels of
38 species richness (2- and 4-species mixtures). They were thus able to demonstrate that
39 physical complementarity does indeed promote ecosystem functioning.

40 In order to do so, Williams et al first established dense experimental stands of young
41 trees with two or four species. Importantly, they also created a gradient in the degree of
42 differences among species within communities of equal species richness. This approach
43 allowed Williams et al. to show that biomass overyielding in mixtures compared with the
44 average monoculture of the species making up the mixtures can be predicted from *a-priori*
45 differences between species in crown architecture and thus vertical space use. Plasticity of
46 species in response to interspecific competition in mixture can increase or decrease physical
47 crown complementarity and this is associated with corresponding modifications of stand
48 biomass (Fig. 1). Direct analysis of physical complementarity between species, before (in
49 monoculture) and after plastic adjustment (in mixed plots), can move biodiversity–ecosystem
50 functioning research beyond the statistical description of species richness and
51 complementarity effects⁴ and beyond modeling⁵ to a more predictive science, permitting
52 better design of forests that can promote biomass production, carbon storage and thus
53 contribute to climate change mitigation.

54 In their analysis, Williams et al. performed a systematically designed experiment with
55 monoculture and mixed communities rather than studying natural tree communities. Such
56 “artificiality” is crucial to reveal mechanisms because one of the basic assumptions of plant
57 biodiversity experiments is that — without interspecific competition — all species could
58 reach constant final yield in mixed plots, in the same way as they could at lower density in
59 monocultures⁶ (dashed frames in Fig. 1). Physical complementarity can be calculated by
60 averaging pairwise vertical crown overlap between trees (independent of whether they are
61 direct neighbours or not). This allows derivation of crown complementarity indices within

62 (CCI_{mono}) and between species as predicted without plasticity (CCI_{pred}) and as observed with
63 plasticity (CCI_{obs}). Williams et al. found that CCI_{pred} and CCI_{obs} were positively correlated
64 with aboveground biomass overyielding, demonstrating that physical crown complementarity
65 determined the degree to which mixed experimental stands exceeded biomass production of
66 monocultures (solid frames in Fig. 1).

67 The mechanisms underlying overyielding have often been analysed statistically,
68 attributing effects to “complementarity effects” and “selection effects”⁴. Interestingly,
69 Williams et al. found that the effect of crown complementarity on overyielding was related
70 mostly to selection effects rather than to complementarity effects³. This suggests that in this
71 case the statistical selection effect included a strong “trait-dependent complementarity
72 effect”⁷, i.e. large trees benefitted from reduced competition from small neighbours, but these
73 smaller trees suffered less than the larger ones benefitted. As hypothesized above, large trees
74 were thus unable to fill all vertical space available to small trees. Another recent study
75 showed that plasticity increased crown overlap (and decreased statistical complementarity
76 effects) in mixed stands of young trees where species were similar in size but decreased
77 crown overlap (and increased statistical complementarity effects) when they differed in size⁸.
78 This might help to explain why Williams et al. found that crown plasticity sometimes
79 decreased and sometimes increased CCI_{obs} relative to CCI_{pred}.

80 Additional dimensions of physical complementarity could conceivably have
81 contributed to biomass overyielding in Williams et al.’s study, for example complementarity
82 in belowground resource use. Furthermore, at least the plastic component of crown
83 complementarity could have been affected by the biomass overyielding itself⁵. Unfortunately,
84 it is impossible to differentiate between such primary and secondary effects. A decisive test
85 would require a set of species that differ in crown architecture only, which cannot reasonably
86 be expected because of the inherent correlations of morphological and physiological traits

87 that emerge from fundamental trade-offs. One might maintain that only effects that cannot be
88 explained by other variables (including biomass overyielding) are causal effects⁵, but this
89 extremist perspective ignores that the opposite may equally be true, i.e. the same reasoning
90 could be applied to these other variables.

91 To understand the biological mechanisms that drive overyielding in mixed
92 communities, experimental research must move from pure species richness manipulations
93 and the assessment of statistical selection and complementarity effects to manipulations of
94 physical complementarity and the analysis of why at a given species richness some mixtures
95 overyield considerably whereas others do not. Manipulations of functional diversity and trait-
96 based approaches have been leading the way, but are usually focused on static species traits
97 that are then used to derive community-weighted trait means and functional diversity
98 measures. It will be interesting to see to what extent plastic responses of species to variation
99 in the diversity and structure of their environment will relate to statistical selection and
100 complementarity effects, even if the conclusion might be that the statistical approach is of
101 limited use and novel approaches will have to be developed to better understand the
102 fundamental mechanisms underlying biodiversity–ecosystem functioning relationships.

103 Williams and colleagues' work has important implications for agriculture and forestry
104 as well, where current production systems mostly consist of monocultures. It may now be
105 possible to identify particular phenotypes that optimally complement each other in the use of
106 resources, allowing the design of forest plantations that deliver higher yields. It is likely that
107 the full potential of such systems of mixed species or provenance up to now has not been
108 recognized and that opportunities to promote desirable ecosystems services such as carbon
109 sequestration are therefore missed.

110

111 1 Cardinale, B.J. *et al.* The functional role of producer diversity in ecosystems.

112 *American Journal of Botany* **98**, 572-592 (2011).

113 2 Vojtech, E., Loreau, M., Yachi, S., Spehn, E.M., Hector, A. Light partitioning in
 114 experimental grass communities. *Oikos* **117**, 1351-1361 (2008).

115 3 Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B. Species
 116 complementarity in tree crowns explains overyielding in species mixtures. *Nature*
 117 *Ecology & Evolution* **x**, xx-xx (2017).

118 4 Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity
 119 experiments. *Nature* **412**, 72-76 (2001).

120 5 Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M. Tropical tree
 121 diversity enhances light capture through crown plasticity and spatial and temporal
 122 niche differences. *Ecology* **95**, 2479-2492 (2014).

123 6 He, J.-S., Wolfe-Bellin, K.S., Schmid, B., Bazzaz, F.A. Density may alter diversity–
 124 productivity relationships in experimental plant communities. *Basic and Applied*
 125 *Ecology* **6**, 505-517 (2005).

126 7 Fox, J.W. Interpreting the ‘selection effect’ of biodiversity on ecosystem function.
 127 *Ecology Letters* **8**, 846-856 (2005).

128 8 Niklaus, P.A., Baruffol, M., Schmid, B. Can niche plasticity promote biodiversity–
 129 productivity relationships through increased complementarity? *Ecology*, *in press*.

130

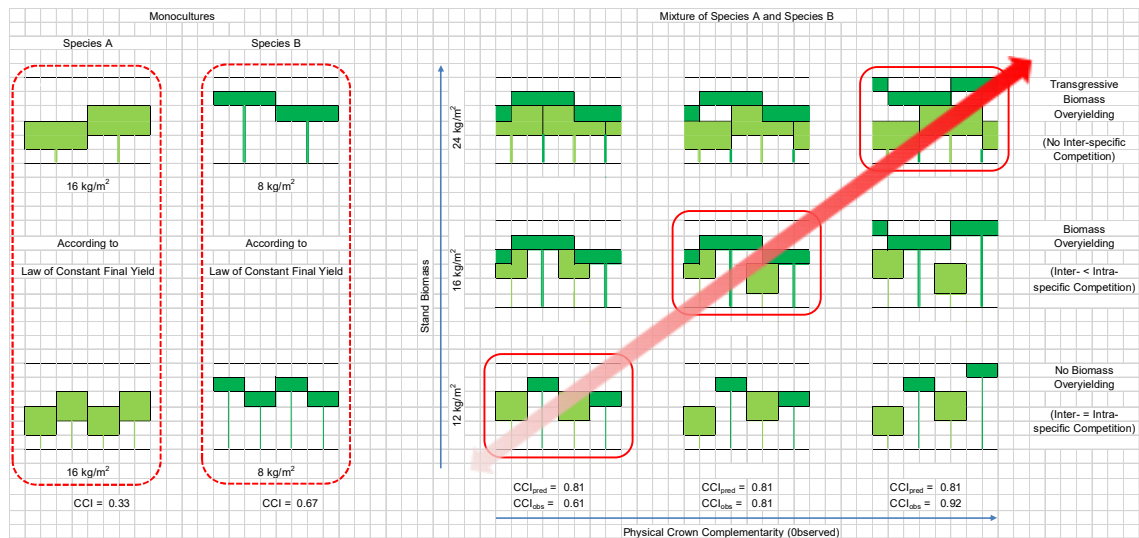


Figure 1 | Illustration of potential effects of crown complementarity between two species in vertical space on stand biomass. The vertical extent of the tree crowns in the pictures is used to calculate crown complementarity indices (CCIs)³ whereas the green crown areas illustrate biomass. The total number of trees planted in monocultures (shown on the left) and mixed stands (shown on the right) is kept constant and therefore the individual density of each species in two-species communities is half the one of monocultures. However, in the absence of interspecific competition each species would produce a biomass equal to monocultures (law of constant final yield) and as a consequence the mixture would produce a total biomass equal to the sum of the two monocultures (top row). With identical inter- and intra-specific competition, the community biomass of the mixture would equal the average biomass of the monocultures (bottom row). The study by Williams et al.³ showed that with reduced vertical overlap, i.e. increased crown complementarity, biomass overyielding in mixtures increased as indicated by the stands in the solid red frames. Plasticity either decreased (first column with mixtures) or increased (third column with mixtures) observed crown complementarity and as a consequence decreased or increased stand biomass.